Patterns of brood production in the grass shrimp *Palaemonetes pugio* (Decapoda: Caridea)

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Summary

The pattern of brood production was analyzed in the grass shrimp *Palaemonetes pugio*. Determination of patterns of brood production as successive (spawning after each molt) or alternate (spawning after every other molt) was made by observations on individual females paired with males in the laboratory over a four-month period. A pattern of successive parturial (spawning) molts was the most common pattern. However, in a majority of these successive parturials, the ovary of the female was not mature at hatching of embryos from a previous brood. There was a delay of 10–11 days, during which ovarian maturation took place, between embryo hatching and the next (parturial) molt. This pattern of "slow successive" parturials does not result in the truly continuous brood production which occurs in many caridean species, i.e., spawning of a new brood within 1–2 days after hatching of a previous brood. However, there was a relatively low percentage of females in which the ovary was mature at embryo hatching. These latter females did have a parturial molt after only 2 days ("fast successive" parturial). In the "alternate" pattern, more frequent later in the 4-month observation period, hatching of embryos was followed by a non-parturial (without spawning) molt within 2 days, followed by an intermolt period of 10 days during which ovarian maturation occurred prior to the next (parturial) molt. The interval between spawns was similar in the "slow successive" and "alternate" parturial molt patterns (22–23 days) compared to a much shorter one (14–15 days) in the "fast successive" parturials. Examination of reproductive females from field samples indicated that the spawning pattern observed in the laboratory was that which occurs in natural populations in southern Louisiana. Although brood production in *P. pugio* is not truly continuous, the relatively short interspawn intervals observed still allow production of several broods during the breeding season.

Key words: Incubation, interspawn interval, molting, ovarian maturation, parturial, spawning

Introduction

The number of spawnings during the annual breeding season is one important component of the total reproductive effort of individuals and, collectively, of the population. In caridean shrimps, females are receptive to mating just after a molt that precedes spawning (parturial or spawning molt). In carideans and other crustaceans, the time interval

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between spawns is an important selective pressure in the evolution of various male mating tactics since it determines, in part, the frequency of females in the population which are available to males for mating (Wickler and Seibt, 1981).

Females of caridean shrimp species attach spawned and fertilized eggs below the abdomen, as do all pleocyemate decapods (Burkenroad, 1963). The brood is then incubated by the female until hatching of the embryos as larvae. Prior to spawning, the ovary undergoes a "maturation" in which the oocytes pass through primary and secondary vitellogenesis. Before spawning, the female undergoes a parturial molt at which morphological characters associated with incubation of the embryos ("breeding dress," Höglund, 1943) are attained for the first time in the breeding season or renewed if the spawning is not the first of the season. Just after the parturial molt, mating takes place and then spawning occurs within minutes, hours, or at most a day or two (Höglund, 1943; Burkenroad, 1947; Bauer, 1976, 1979; O'Donovan et al., 1984; Bauer and Holt, 1998; Bauer and Abdalla, 2000).

Many caridean females are "continuous" or "successive" breeders, i.e., they produce a new brood very soon after a previous brood of embryos has hatched (Bauer, 1976, 1979, 1989; O'Donovan et. al., 1984; Bauer and Holt, 1998). In this pattern of multiple brood production, the ovary matures again as the incubated embryos of a previous spawning develop. When the embryos hatch, the ovary is mature (full of vitellogenic oocytes) and ready for spawning. Within a day or two of embryo hatching, the female undergoes a parturial molt, mates immediately or shortly thereafter, and soon spawns again. Thus, the interspawn interval of such "continuous" breeders corresponds to the incubation period of embryos from the previous spawn plus one to a few days during which a parturial molt, mating, and spawning take place. In continuous breeders, females which are carrying embryos near hatching have a mature, prespawning ovary. Since such individuals will hatch embryos and undergo a parturial molt within a short time (a few days or less), they can be selected for use in observations and experiments on mating and spawning (Bauer, 1976, 1979; Bauer and Holt, 1998).

Continuous (successive) breeding has been reported in females of many caridean species, e.g., in tropical and subtropical seagrass species (Bauer, 1986, 1989, 1992; Bauer and VanHoy, 1996), *Heptacarpus sitchensis* and *H. paludicola* from the west coast of the US (Bauer, 1976, 1979), and *Macrobrachium rosenbergii*, a species from Southeast Asia (Wickins and Beard, 1974; O'Donovan, 1984). In some carideans, however, ovarian maturation takes two molting cycles (Bouchon et al., 1992), so that if more than one brood is produced per breeding season, spawning can only take place at every other molt ("alternately" rather than "successively"). At the other extreme are species in which females produce but a single brood per year, particularly cold-water carideans such as boreal pandalids (Allen, 1966; Butler, 1980; Williams, 1984).

In the brackish and freshwater genus *Palaemonetes*, different patterns have been reported. Based on qualitative observations on the presence of mature ovaries in many females incubating embryos, Knowlton and Williams (1970) stated that breeding was continuous in *P. vulgaris*. Beck and Cowell (1976) observed in *P. paludosus* that many females carrying embryos also had mature ovaries, suggesting successive broods. Spivak (1997) and Schuldt and Damborenea (1987) gave similar evidence from field samples suggesting two to three successive broods in at least some females of *P. argentinus*. Jeffries (1964) followed females of a cool-temperate species, *P. varians*, in the laboratory and found that only a small percentage had more that one brood, with a intervening non-parturial molt between the first and second parturial molts and spawnings.

The objective of this present study was to describe in detail the patterns of brood production in females of *Palaemonetes pugio*, an abundant and ecologically important estuarine caridean shrimp species along the US Atlantic and Gulf coasts. The relationship of ovarian development, molting, spawning, and interspawn intervals are described. Field and laboratory observations on brood production were used to test the hypothesis that spawning is continuous in *P. pugio*, i.e., females produce successive broods with a parturial (spawning) molt soon after hatching of a previously incubated brood. The alternative hypothesis examined was that brood production is not continuous, with one or more non-parturial molts between spawnings.

Materials and Methods

Collections of *P. pugio* for laboratory observations on spawning and molting were made at Cypremort Point, Louisiana, USA (29°43'N, 91°51'W) in April, 1996. Preserved specimens of brooding (embryo-carrying) females on which observations of ovarian condition were made were selected from field samples taken twice monthly from April through September (breeding season) 1999 at Grande Terre Island, just off

the east end of Grand Isle, Louisiana (29°15′N, 89°57′W). Females from collections taken in July, 1987, and April, 1988, from the Cocodrie Marsh, Louisiana (29°14′N, 90°39′W) were also examined.

Breeding patterns of 24 individual females, each continuously paired with a male, were observed for four months (mid-April to mid-August, 1996). Female–male pairs were kept in plastic containers, perforated to allow water circulation, on a laboratory water table supplied with recirculating seawater of 4–6 ppt salinity, similar to that found at the collecting site and within the "optimal" salinity range reported for *P. pugio* by Anderson (1985). Water temperature was maintained throughout the observations at 27–28°C, within the mid-range of breeding temperatures (Anderson, 1985). The light:dark cycle was kept at 14 h:10 h, the longest natural daylength at the latitude at which the shrimps were collected. Shrimps were fed daily with commercial fish food (shrimp pellets). Daily observations were made on breeding characteristics and molting of females. The presence or absence of a female exuviae and a brood of embryos below the female's abdomen was recorded. In addition, the degree of ovarian maturation (filling of ovary with large vitellogenic oocytes) was estimated visually, without magnification or handling, through the transparent cuticle of the female, as follows: stage 1, no evidence of ovarian development; stage 2, ovary apparent but small, not extending forward into the space above the cardiac stomach in the anterior half of the cephalothorax; stage 3, ovary large, extending into space above the cardiac stomach but not filling more than half that space; stage 4, ovary large and full, filling most or all of space above the cardiac stomach. In preserved material in which vitellogenic oocytes in the ovary can be clearly observed using a stereomicroscope, these stages correspond to those used to estimate ovarian maturity (nearness to spawning) in Bauer and Holt (1998) and Bauer (1986): stage 1, no observable vitellogenic oocytes in the ovary; stage 2, vitellogenic oocytes distinct but ovary small, not or barely extending into the cephalothoracic space above the cardiac stomach; stage 3, ovary with vitellogenic oocytes filling at least half the space above the cardiac stomach; stage 4 ("mature"), ovary with vitellogenic oocytes extending nearly or completely filling that space.

In samples from field collections, the degree of ovarian maturation (stages 1–4) in females brooding embryos near hatching was observed and recorded. Embryos near hatching have well developed eyes, limbs are developed, the abdomen is free from the rest

of the body, and there is little or no visible yolk, as in Bauer and Holt (1998) and Bauer (1986).

Results

Molting and spawning patterns from long-term observations on individual females

The 24 females individually paired with males went through a total of 107 parturial (spawning) molts, with a median of four parturial molts per female [95% confidence limits (c.l.): 4,5; minimum = 3, maximum = 7]. Of the 107 parturial molts and spawns, 72% were successive (without an intervening non-parturial molt), 23.4% followed an alternate pattern (with one non-parturial molt between spawns) and for 3.7% ("other"), two or more non-parturial molts occurred between spawning molts (Figs. 1, 2). Successive spawnings occurred more frequently in the first two months of observations, after which alternate and other parturial molt patterns became frequent as well (Fig. 2). The increased frequency of alternate and other parturial molts with time is demonstrated by dividing the observation period into two parts: 0–63 days and 64–126 days. In the 0–63-day period, only 56 of 59 parturial molts were successive, three were alternate and none were "other," while in the 64–126-day period, 22 of 48 parturials were successive, 22 were alternate and four were "other". The hypothesis that the frequency distribution of parturial molt types in the 0–63-day period is not different from that of the 64–126-day period was tested with a χ-square, using expected frequencies for the 0–63-day period calculated from those observed in the 64–126-day period, in which all types of parturial molts occurred. The hypothesis of no difference in parturial molt type frequency between the two periods is rejected (χ-square, $2 df = 57.03$, $p \ll 0.005$).

The interval between parturial molts, or interspawn interval, could be determined for 83 of the 107 parturial molts (the spawning date of the brood incubated prior to the first observed parturial molt of each female was unknown) (Fig. 2). The median interspawn interval was 23 days (95% c.l.: 22,24; minimum = 13, maximum = 55). Interspawn intervals of successive and alternate patterns were similar, with medians of 22 days (95% c.l.: 21,23; $n=54$) and 23 days (95% c.l.: 22,25; $n=25$), respectively. The hypothesis of no difference in median interspawn interval between successive and alternate patterns, tested with the Mann-Whitney rank sum test is accepted ($p = 0.57$). In the four "other" parturial molts,
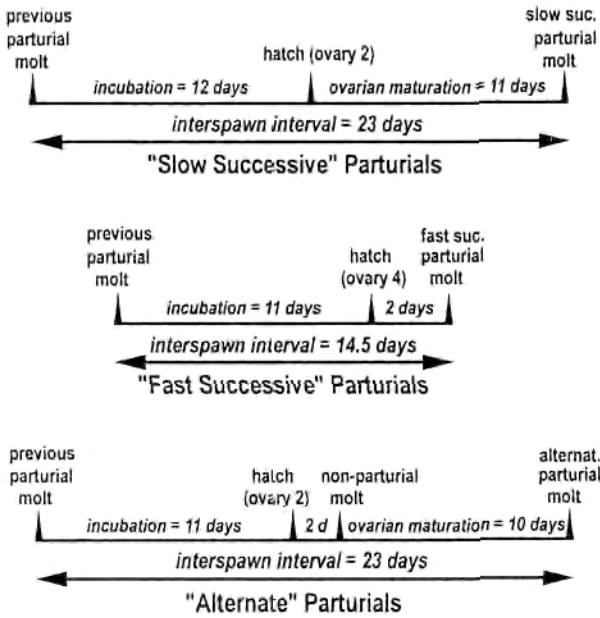
Fig. 1. Schedule of molting, spawning, embryo incubation, hatching, ovarian maturation in the principal patterns of brood production in *Palaemonetes pugio*. Median values are given for interspawn and other time intervals. For the "fast successive" parturial pattern, medians for incubation period and the period from hatching to the next parturial molt do not add up to the median for the interspawn interval because of variation within these variables.

Fig. 2. Interval between spawns for successive ("S"), alternate ("A") and other ("O") patterns of parturial molts ($n = 83$) plotted against time from the start of long-term laboratory observations on 24 females individually paired with males.

the median was 43 days (minimum = 33; maximum = 55).

The interspawn interval can be divided into (1) the incubation period (spawning to hatching of embryos) and (2) the period between hatching and the next parturial molt in the successive pattern of parturial molting, or, in the alternate pattern, the periods (a) between hatching and the non-parturial molt and (b) between the non-parturial and the next parturial molt (Fig. 1). Overall, the median incubation period was 11 days (95% c.l.: 11,12; min = 7, max =23; n = 104 broods). The median and 95% c.l. for incubation period was the same for successive and alternate spawns, and the hypothesis of no difference is accepted ($p = 0.194$; Mann-Whitney test).

In the successive pattern, the median time from hatching of a previous brood to the next molt (a parturial one) was 10 days (95% c.l.: 9,11; min = 0, max = 33; n = 78). In the alternate pattern, the next molt after hatching of a brood was a non-parturial molt, which took place quickly within a median of 2 days (95% c.l.: 1,2; min = 0, max = 7; n =25). The difference in median time from hatching to next molt
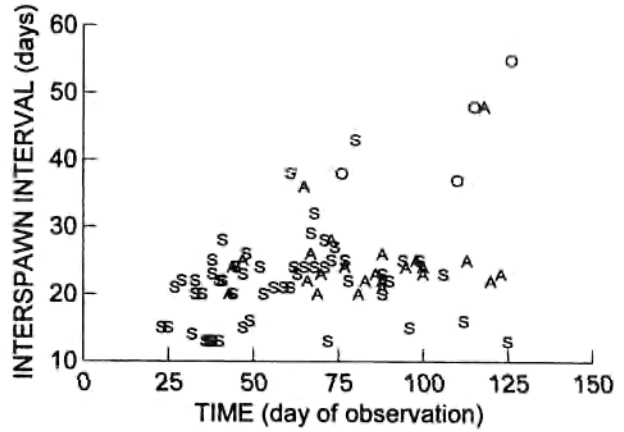
between successive (hatching to parturial) and alternate spawns (hatching to non-parturial) is statistically significant ($p < 0.001$; Mann-Whitney test). In the alternate pattern, another 10 days passed between the non-parturial molt and the next parturial molt and spawn (interspawn interval of 23 days minus 11 days incubation period = 12 days minus 2 days to non-parturial molt = 10 days from non-parturial to next parturial molt).

At the hatching of a brood of embryos, the female's stage of ovarian development, an indicator of nearness to the next spawn, varied from 1 (no ovarian development) to 4 (ovary mature, ready to spawn), with a most frequent value of 2 (ovary with some observable vitellogenic oocytes) (Fig. 3). When female ovarian condition at hatching of the previously-spawned brood is compared between successive and alternate parturial molts, the median was 2 for both successive (95% c.l.: 2,3; min = 1, max = 4; n = 78) and alternate (95% c.l., 1,2; min = 1, max =2; n =25). However, due to the considerable variation in ovarian condition at hatching of a previous brood in successive parturial molts, the hypothesis of no difference in median ovarian stage at hatching between successive and alternate parturials is rejected ($p < 0.001$; Mann- Whitney test).

The considerable variation in values for the interspawn period, period from hatching to next molt, and ovarian condition associated with successive spawns was analyzed further. In 13 of 78 (16.7%) successive parturial molts, the female had a stage 4 ovary, i.e., an ovary full of vitellogenic oocytes, at hatching of the prior brood. In such females, the successive parturial
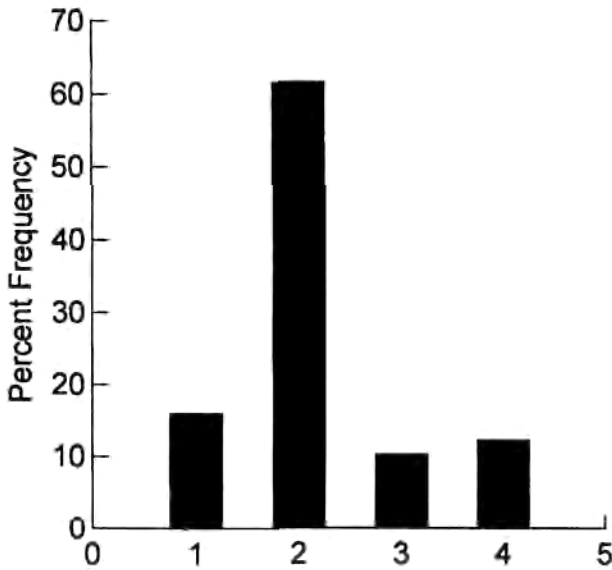
Fig. 3. Stage of ovarian maturation of laboratory females upon hatching of brooded embryos ($n = 107$ broods).
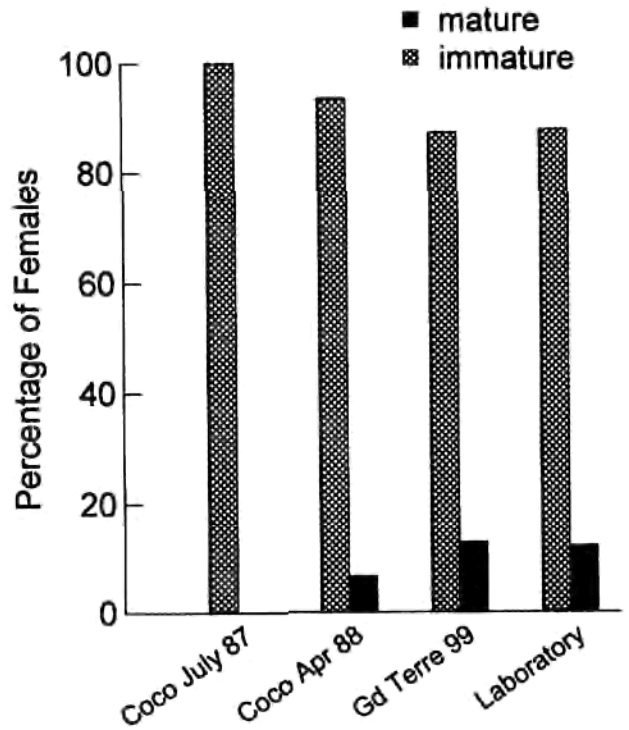

Fig. 4. Stage of ovarian maturation of females carrying embryos near hatching from three field collections compared to that of laboratory females at the time of hatching. Coco = Cocodrie Marsh; Gd Terre = Grand Terre Island; immature = ovarian stages 1–3; mature = ovarian stage 4.

molt was "fast," with the median time from hatching to the next parturial molt only two days (95% c.l.: 0,3; min = 0, max = 5; $n = 13$) (Fig. 1). In contrast, in females with stage 1–3 ovarian condition at hatching, the successive parturial molt was "slow," with a median time from hatching to the next parturial molt of 11 days (95% c.l.: 10, 24; min = 0, max = 33, $n = 65$) (Fig. 1). The difference between "fast" and "slow" successive parturials in median time from hatching of the previous brood to the parturial molt is significant ($p < 0.001$; Mann-Whitney test). The interspawn interval was correspondingly shorter for the "fast" successive parturials, with a median of 14.5 days (95% c.l.: 13,20; min = 13, max = 24; $n = 12$) compared to a median of 23 days for "slow" successive parturials (95% c.l.: 22,24; min = 13, max = 43; $n = 42$). These medians are significantly different ($p < 0.001$; Mann-Whitney test). Incubation of broods took a similar time in both groups, with a median of 11 days for "fast" successive parturials (95% c.l.: 10,12; min = 10, max = 12; $n = 12$) and 12 days for "slow" ones (95% c.l.: 11, 12; min = 7; max = 23; $n = 62$). These medians are not significantly different ($p = 0.117$; Mann-Whitney test).

Spawning patterns inferred from field samples

It was shown in laboratory observations above that females with a mature ovary (stage 4) at hatching of incubated embryos would spawn again within a few days ("fast successive" parturial molts). To estimate the frequency of such continuous breeding in

populations from nature, field samples of *P. pugio* from Cocodrie Marsh and Grand Terre, Louisiana, were examined. The ovarian condition of females carrying embryos near hatching (large eyes, free abdomen, little or no yolk) was examined. In samples from Cocodrie Marsh in July, 1987, 100% of females ($n = 77$) with embryos near hatching had immature (stages 1–3) ovaries (Fig .4), so that the next parturial molt would be either a "slow successive" or "alternate" one. In the April, 1988, Cocodrie Marsh sample, 93.5% of females ($n = 77$) incubating broods near hatching showed this pattern, but 6.5% had mature (stage 4) ovaries, indicating a "fast successive" parturial molting (Fig. 4). In samples taken from April through September, 1999, at Grand Isle, Louisiana, 118 females carrying broods near hatching were taken. Of these, 12.7% had mature ovaries, indicating a parturial molt within days of hatching of the brooded embryos, while 87.3% of females with embryos near hatching showed immature ovaries, indicating that the next parturial would be either a "slow successive" or an "alternate" one (Fig. 4).

In order to compare the frequency of "fast successive" parturials between females from field

samples and females maintained in the laboratory and followed through multiple spawns, the ovarian condition at embryo hatching of laboratory females was grouped into "immature" (stages 1–3) and "mature" (stage 4). A mature ovary was present in 12.1% of laboratory females (*n* = 107 observations) at hatching of a brood prior to the parturial molt, an indication of the "fast successive" parturial molt pattern (Fig. 4).

Discussion

Although the majority of parturial (spawning) molts occurred successively, one after the other without an intervening non-parturial molt, brood production in the populations of *P. pugio* examined cannot be called truly continuous. In carideans with continuous brood production, the ovary of a female fills with vitellogenic oocytes as it broods embryos from the previous parturial molt and spawn. In such females, the time interval between hatching of one brood, molting, and spawning of the next brood is short, usually 1–2 days (Höglund, 1943; Burkenroad, 1947; Bauer, 1976, 1979; O'Donovan et al., 1984; Bauer and Holt, 1998). Only a relatively small percentage (16.7%) of successive parturial molts followed this "fast" pattern in females of *P. pugio* observed individually for 4 months in the laboratory. In most successive parturial molts, the ovary of the female was not mature at hatching of the previous brood. A relatively long period of about 10 days had to pass before the ovary was mature and the female was ready for the next molt ("slow successive" parturial) and spawning.

A less frequent pattern of molting and spawning was observed in *P. pugio* females maintained in the laboratory in which parturial molts were separated by one non-parturial molt. As in "slow" successive parturials, females showing this "alternate" pattern had immature ovaries at the time of hatching of the previous brood. Within a median period of 2 days, the female underwent a non-parturial molt, followed by a short intermolt period of 10 days in which the ovary matured into spawning condition before the next molt, a parturial one. The median interspawn interval in the "alternate" and "slow successive" spawns were not statistically different.

Examination of females from field samples indicated similar patterns of molting and spawning in natural populations. As in the laboratory females, only a low percentage of females from field samples had mature ovaries when carrying embryos near hatching. Mature ovaries at hatching indicates that females will produce a new brood within a few days after the previous brood hatches ("fast successive" parturial molt). Most females from field samples had immature ovaries at hatching, indicating either a "slow successive" or "alternate" parturial molt pattern. Thus, only a relatively small proportion of *P. pugio* females in populations sampled were "continuous" multiple brooders.

Both laboratory and field observations in our study indicate that the most frequent patterns of molting and spawning are the "slow successive" and "alternate" ones, both of which result in an similar interspawn interval (22–23 days). Based on these results, we estimate that in a breeding season from April through September (180 days), a *P. pugio* female from the warm-temperate waters of the northern Gulf of Mexico should produce eight broods (180 days/22.5 days between spawns). This is a considerable number compared to that reported during the entire breeding seasons of other species of *Palaemonetes*, ranging from 1, infrequently 2, in the higher latitude *P. varians* (Jeffries, 1964) from the British Isles to 1–3 in the warm temperate *P. argentinus* (Schuldt and Damborenea, 1987; Spivak, 1997) from Argentina. Knowlton and Williams (1970) stated that in North Carolina, females of *P. vulgaris* and *P. pugio* with embryos near hatching had mature ovaries, indicating spawning again soon after hatching (continuous reproduction). However, this statement needs verification since no data were presented in that short publication (abstract).

In studies on the caridean shrimp *Macrobrachium nobilii*, Pandian and Balasundaram (1982) have pointed out that a reproductive female's energy supply is channeled into somatic growth (net somatic growth plus exuviae production) and egg production. The way in which the energy supply may be apportioned apparently varies among caridean species, with several patterns possible. It seems puzzling that a prolific, abundant caridean such as *P. pugio* is apparently incapable of increasing its reproductive output by more frequently using the "fast successive" parturial molt pattern which results in more frequent brood production. Many species of carideans similar or smaller in size than *P. pugio* are capable of continuous, frequent brood production, e.g., tropical seagrass carideans (Bauer, 1989). Species of large body size from the same family as *P. pugio*, e.g., the palaemonid *Macrobrachium rosenbergii*, are also capable of truly continuous brood production (Wickins and Beard, 1974). It is difficult to hypothesize what adaptive advantage the "slow successive" and "alternate" parturial patterns have over the "fast successive" pattern in *P. pugio*. There may be some environ-

mentally imposed energetic constraints which prevent *P. pugio* from utilizing the more productive "fast successive" parturial pattern (continuous brood production) more often. It can be proposed that a lag between hatching and the next parturial molt ("slow successive" pattern) or between the non-parturial molt and next parturial molt ("alternate" pattern) allows *P. pugio* females to devote more energy to both growth and reproduction. However, in other species of the same family, such as *M. rosenbergii*, females are capable of both considerable growth and considerable egg production while continuously producing broods, one after another, with only a short period between hatching of one brood and spawning of the next.

Acknowledgments

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